The Australasian Protocardiinae revisited (Bivalvia: Cardiidae)

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Abstract. The Protocardiinae, the oldest unquestionable group of the family Cardiidae, has a long geological existence in Australasia. Six Recent Australasian species have been recognized and are traditionally referred to *Nemocardium s.l.* Two of them belong to *Pratulum*, a genus-group now restricted to relatively deep biotopes in warm temperate waters of Australasia. Considering its characteristic sculptural pattern and restricted Australian-New Zealand distribution since the Cretaceous, *Pratulum* is considered here to be a distinctive genus. The genera *Microcardium* and *Trifaricardium* are reported for the first time from Australasia. The other Australian species of Protocardiinae are classified in *Lyrocardium* and *Frigidocardium*, with a single species remaining in *Nemocardium s.s.*

Since two new species of *Microcardium* were obtained in the upper bathyal zone by the French oceanographic expedition MUSORSTOM-1 in the Philippine Islands (Poutiers, 1981), further investigations allowed the accumulation of new data on Recent and fossil Cardiidae. This has rendered necessary the publication of a series of papers devoted to this family, and specially to members of the subfamily Protocardiinae. This paper is intended only as a preliminary note on the subject, in which the present author gives some results of his studies on Australasian Protocardiines, and discusses the taxonomy, biogeography and paleontology of the group.

This note is based on an extensive suite of fossil and Recent material from the Indo-Pacific area, including material collected since 1977 during several oceanographic expeditions organised by the Paris Muséum national d'Histoire naturelle (Richer de Forges, 1990) as well as historic and recently collected material obtained from various institutions. Detailed analysis of the material used in this study, and descriptions of new taxa illustrated here will appear in subsequent publications.

Since the subfamily Protocardiinae was established (Keen, 1951), there have been only a few studies on this group as a whole (Keen, 1969, 1980; Habe, 1977; Kafanov and Popov, 1977; Popov, 1977). To date, most authors have adopted the taxonomic scheme advanced by Keen.

FOSSIL RECORD

The protocardiines are the oldest unquestionable representatives of the Cardiidae. Their fossil record extends back to the Upper Triassic and they diversified largely during the Mesozoic. This is especially true for *Protocardia* Beyrich, 1845, the type-genus of the subfamily, which is known from Upper Triassic to Upper Cretaceous. Only one other genus, *Septocardia* Hall and Whitefield, 1877, allegedly belonging to the subfamily Cardiinae, occurs in the Upper Triassic, but its placement in the Cardiidae has not received a general acceptance among taxonomists (Kafanov and Popov, 1977). Two taxa, *Nemocardium* Meek, 1876, and *Pratulum* Iredale, 1924, bridged the gap between Mesozoic and Cenozoic (Keen, 1950, 1980; Skwarko, 1983), and they still occur in the Recent fauna. They are the only members of the family to show this stratigraphic distribution. After a second period of radiative evolution during the Tertiary, Protocardiines nowadays survive mainly on the outer shelf and upper continental slope. This is a rather deep-water habitat for the family that occurs typically in the shallow waters of coastal to subtidal environments. Thus, in a way, Recent Protocardiines can be considered as a relict deep-water group within the family Cardiidae.

BIOGEOGRAPHY

The subfamily Protocardinae is present in nearly every tropical region, and the western Pacific Ocean is the area of maximum species diversity with 15 of the 26 known species worldwide (Fig. 1). The genus *Microcardium* Thiele, 1934, is a good example. No less than three species are known from Philippine waters, two of which have been described recently (Poutiers, 1981). The most common of these, *Microcardium aequiliratum* Poutiers, 1981 (Fig. 2a), lives in fine soft bottoms at depths of 180m to 350m. In addition to the Western Pacific Ocean, Protocardiines occur also in the Indian Ocean (six species), Eastern Pacific (five species), as well as in the Western and Eastern Atlantic Ocean (three and one species respectively).

In Australasia, five Recent species of Protocardiines are known from Australia (two of which occur also in New

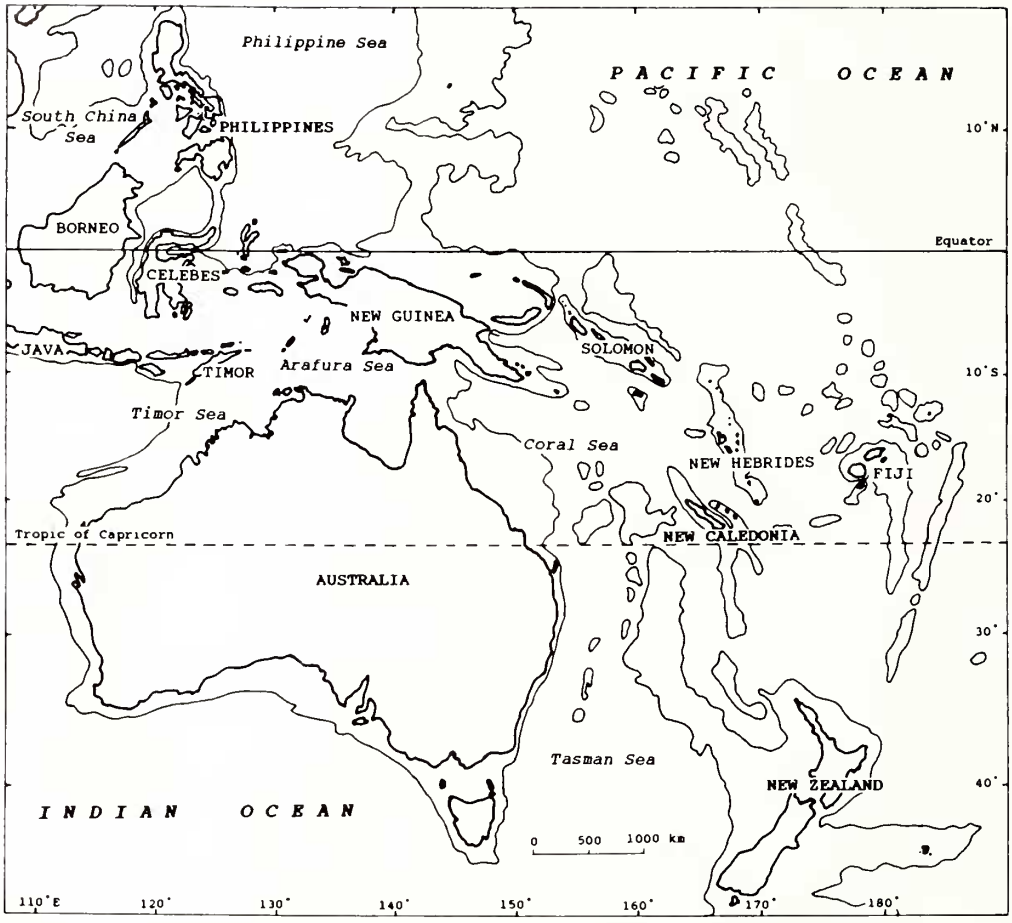

Fig. 1. Simplified map of Australasia and neighbouring areas.

Caledonia), and one from New Zealand. They are traditionally allocated to the broadly defined genus *Nemocardium*, as are all Recent species of the Protocardiinae (Keen, 1969, 1980). This placement seems to be supported by the rather conservative aspect of conchological characters in the subfamily, and by a frequent occurrence of secondary convergence that makes the differentiation of lineages sometimes problematical.

According to the climatic zonation of the world oceans, two main biogeographical areas are recognized currently in Australasia. In these areas, a number of faunal regions and provinces have been defined for the intertidal and shelf zones, on the basis of distribution and the degree of endemism of the benthic and demersal organisms (Wilson, 1971; Briggs, 1974; Pielou, 1979). Thus, northern Australia, New Caledonia and its dependencies (Fig. 1) are included in the tropical Indo-West Pacific Region, whereas southern Australia and northern New Zealand correspond to a warm temperate area forming the Southern Australian and the Northern New Zealand Regions.

This biogeographical pattern is reflected in the distribution of Protocardiines in Australian waters. *Nemocardium* is present in the tropical region, represented by *N. bechei* (Reeve, 1840), the only living species of *Nemocardium s.s.* (Fig. 2b). *Pratulum* occurs in the temperate region, represented by *P. thetidis* (Hedley, 1902), type-species of the genus (Fig. 2c). *P. thetidis* was thought by Hedley (1902) to be only a local variety of *Cardium striatulum* Sowerby, 1834, an older but incorrect name for the New Zealand species *P. pulchellum* (Gray, 1843) (Fig. 2d). However, Iredale (1924) correctly distinguished these species when he erected *Pratulum*.

Pratulum appears to be confined nowadays to the temperate waters of Australasia. The only record of *Pratulum* from tropical Australasia is that of Fischer-Piette (1977). This seems to be an error based on the incorrect labelling of an old specimen, and I have been unable to find any member of this genus in the large samples collected recently in that region by the Paris Muséum national d'Histoire naturelle. However, paleontologists often consider *Pratulum* a Tethyan Indo-Pacific element, like *Nemocardium s.s.* For example, Darragh (1985), using a similar approach to Fleming (1962, 1967), analysed the composition of the molluscan fauna to define a tentative biozonation of the Tertiary in southeastern Australia and included *Pratulum* under the Tethyan Indo-

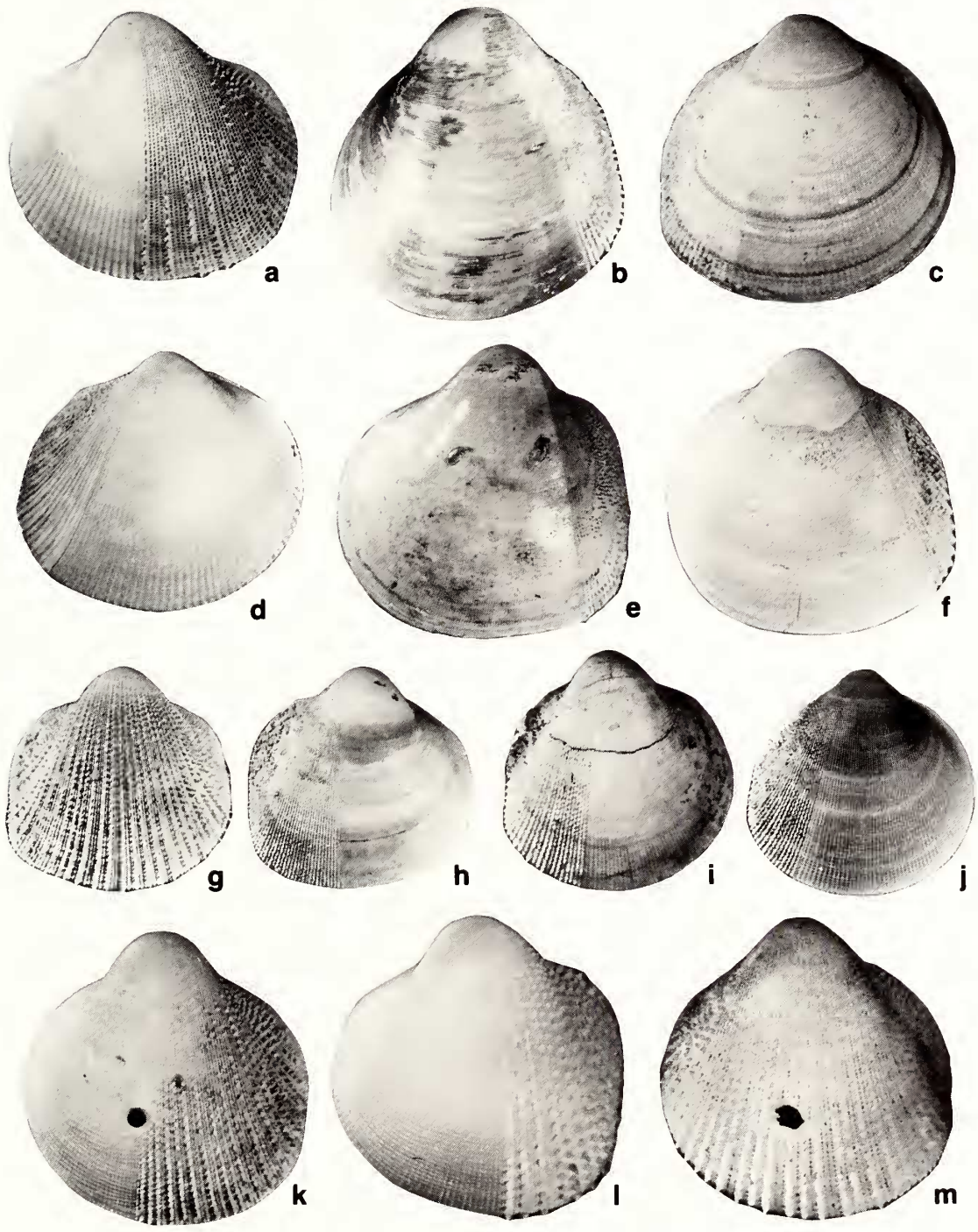

Fig. 2. External views of Recent and Tertiary species of Protocardiinae, showing diversity of sculpturing among genera (AMS, Australia Museum, Sydney; MNHN, Muséum national d'Histoire naturelle, Paris; MV, Museum of Victoria, Melbourne). **a)** *Microcardium aequiliratum*, length 26.5 mm, Philippines, MUSORSTOM-2 Stn 17 (MNHN); **b)** *Nemocardium bechei*, length 40.0 mm, New Caledonia Stn 542 (MNHN); **c)** *Pratulum thetidis*, length 16.0 mm, southern Australia (AMS C145776); **d)** *P. pulchellum*, length 22.0 mm, New Zealand (MNHN); **e)** *N. antisemigranulatum*, length 39.2 mm, middle Miocene of Australia (MV P128253-57); **f)** *N. edwardsi*, length 50.1 mm, Paleocene of Paris Basin (MNHN); **g)** *Frigidocardium sp.*, length 10.9 mm, middle Miocene of Australia (MV P123418); **h)** *P. hemimeris*, length 8.6 mm, middle Miocene of Australia (MV P123419); **i)** *P. ornithopetronicum*, length 11.4 mm, upper Oligocene of Australia (MV P123422-36); **j)** *P. proterothetidis*, length 12.4 mm, Pliocene of Australia (MV P30788); **k)** *Microcardium sp. A*, length 11.1 mm, northwestern Australia (AMS C145746); **l)** *Microcardium sp. B.*, length 11.3 mm, New Caledonia, MUSORSTOM-6 Stn DW428 (MNHN); **m)** *Trifaricardium sp.*, length 11.6 mm, northeastern Australia (AMS C145814).

Pacific heading, but did not record *Nemocardium* from that region. Therefore, a re-evaluation of the generic status of Australian species seemed necessary to decide if there is any correlation between the past and the present biogeography of Protocardiines.

TAXONOMY

Nemocardium s.s. is well known from Cenozoic strata. It is a typical Tethyan Indo-Pacific element, with maximum species diversity in the Paleogene of Europe, where about 30 nominal species are recorded (Keen, 1950; Tremlett, 1950; Popov, 1977). *Nemocardium* exhibits a characteristic, strongly discrepant, outer sculpture with well marked radial ribs on the posterior area; the remainder of the surface is quite smooth and reveals only numerous, fine and low subsurface radial riblets. Internally, the marginal crenulations appear much stronger on the posterior area, in accordance with the outer radial sculpture. On the posterior margin, crenulations correspond with radial ribs but, on the ventral and anterior margins, they correspond with interstices.

In the Cenozoic of New Zealand, *Nemocardium* is represented by *Varicardium* Marwick, 1944, known from the Upper Eocene to the Middle Miocene (Beu and Marwick, 1990). Species of *Varicardium* have been first referred to the Mesozoic genus *Protocardia* (Suter, 1914; Finlay, 1924) in view of the concentric folds of their anterior slope. However, as already pointed out by Marwick (1944) himself, it appears to be a case of secondary convergence and *Varicardium* more probably represents an offshoot of the *Nemocardium* line in New Zealand (Boreham, 1965; Keen, 1980).

In Australia, *Nemocardium* is known from the Miocene onwards, represented by the species *N. antisemigranulatum* (McCoy, 1877) (Fig 2e). McCoy (op. cit.) described it as a species of *"Cardium (Protocardium)"*, an unjustifiable emendation for *Protocardia*. However, this latter taxon is confined to the Mesozoic, and Stewart (1930) has given good reasons for separating it from *Nemocardium* at the generic level. Since then, this species has often been classed in *Pratulum* (Darragh, 1970). However, it shows strong affinities with the Recent species *N. bechei*, and with typical *Nemocardium* species from the Paleogene of Europe (Fig. 2f), and fits well in that genus. This kind of confusion in the generic placement of species is rather common in the Protocardiinae. The first confusion between *Nemocardium* and *Pratulum* was due to Iredale (1927) himself, who differentiated the Australian specimens of *N. bechei* under the name *"Pratulum probatum"*, *i.e.* only three years after he created the genus *Pratulum*; the true affinity of *P. probatum* has been shown by Wilson and Stevenson (1977). In addition, Australian Cenozoic Protocardiines are almost invariably referred to *Pratulum*, without any consideration to their true generic status. For example, it was found that collections of the Museum of Victoria contain a Miocene species of the genus *Frigidocardium* Habe, 1951 (Fig. 2g) which had been confused with *P. hemimeris* (Tate, 1887). This seems to be the first fossil record of *Frigidocardium* in Australia. *Frigidocardium* is characterized by an homogeneous outer sculpture, whereas both *Pratulum* and *Nemocardium* exhibit two clearly differentiated areas.

Recent species of *Pratulum* have a distinctive sculptural pattern. As noted above, the outer surface has two clearly differentiated areas as in *Nemocardium s.s.* but, in *Pratulum*, radial ribbing is not confined to the posterior area. Moreover, the anterior and median areas of *Pratulum* spp. have a fine secondary sculpture of irregularly concentric, anastomosing threads crossing the radial ribs. The marginal crenulations are not clearly stronger posteriorly as they are in *Nemocardium* but, as in that genus, the crenulations do correspond with the radial sculpture. The study of Australian fossils reveals that, despite the above mentioned errors in generic placement, *Pratulum* actually is present in Australia during the whole Cenozoic, and probably also in Upper Cretaceous (Skwarko, 1983). The known Australian Cenozoic species referrable to *Pratulum* are: *Cardium hemimeris* Tate, 1887 (Fig. 2h), *Protocardia ornithopetronica* Chapman and Crespin, 1928 (Fig. 2i), *N. (Pratulum) proterothetidis* Ludbrook, 1955 (Fig. 2j). In New Zealand, *Pratulum* also has a long history (Finlay and Marwick, 1937; Marwick, 1944) and there is evidence that it has been present from the Early Paleocene onwards (Hornibrook and Harrington, 1957; Beu and Marwick, 1990). However, none of the Cenozoic European species referred formerly to *Pratulum* actually belong to this genus (Gilbert and Van de Poël, 1970).

Thus, *Pratulum* appears to be a distinctive genus with a mainly Australian-New Zealand distribution, and the claim that it represents a Tethyan Indo-Pacific element seems unfounded. Recent *Pratulum* comprises three species, one in New Zealand and two in Australia (one undescribed).

In spite of morphological similarities between *Partulum* and *Microcardium* Thiele, 1934, the latter seems to be a distinct lineage of tropical affinities, with a completely different history. Its primary diversification center could be Central America. Morphologically, *Microcardium* can be distinguished from *Pratulum* by the occurrence of concentric scales in the interstices of radial ribs of the posterior area. *Microcardium* is here reported for the first time in the extant Australasian fauna, with one new species in Australia (Fig. 2k), and one in New Caledonia (Fig. 2l). There do not seem to be any fossil records of this genus in Australia. *Trifaricardium* Kuroda and Habe, 1951, is also recorded for the first time in that region, with a new Recent species occurring in Australia and the Coral Sea (Fig. 2m). This genus closely resembles *Frigidocardium*, but can be distinguished by its strong, beaded concentric threads on the anterior slope.

The other Australian species of the subfamily Proto-

cardiinae can be referred to *Frigidocardium* (two species) and *Lyrocardium* (one species), with a single species *(Nemocardium bechei)* remaining in *Nemocardium s.s.* In their comprehensive account of Western Australian Cardiidae, Wilson and Stevenson (1977) dealt with these taxa, but described the species of *Frigidocardium* under the heading of *"Nemocardium (Microcardium)"*.

DISCUSSION

If the subfamily Protocardiinae represents a mainly deep-water, relict group in the Recent fauna, it appears to be well diversified in Australasia. The bathymetrical distribution of its member taxa reveals once more the conservative character of the upper bathyal zone (Lozouet, 1990). Moreover, the recent exploration of the bathyal area of South West Pacific around New Caledonia reveals that a number of taxa descend directly from the Mesozoic fauna (Vacelet, 1977; Ameziane-Cominardi *et al.*, 1987; Bouchet, 1987; Bourseau *et al.*, 1987) in this relatively stable, refuge area, which represents a survival of the eastern rim of Gondwanaland. In itself, this new information justifies the efforts of faunistic research made in this region.

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